



NAMRL Technical Memorandum 96-3

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**NAVAL AEROSPACE MEDICAL RESEARCH LABORATORY
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**OTOLITH CONTRIBUTION TO OCULAR TORSION AND SPATIAL
ORIENTATION DURING ACCELERATION**

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ABSTRACT

Humans perceive linear acceleration and tilt by the otoliths as a result of shear forces on the maculae. A paradigm was set up to study the influence of forces from different directions on the otoliths, on eye movements and tilt perception. On the Coriolis Acceleration Platform of the Naval Aerospace Medical Research Laboratory (NAMRL), five adult male subjects were oscillated in the lateral direction (Y-axis, subject either sitting "upright" or "supine") and in the longitudinal direction (Z-axis, subject "supine" or on his right side). A fifth condition, in which the subject was oriented "upright" facing the direction of oscillation (X-axis), served as a control condition. In separate sessions, the same subjects were also rotated in these five orientations. Data were obtained by measuring ocular torsion with video-oculography, and the direction of the subjective vertical was recorded by means of a joystick. The sinusoidal oscillations were at 0.22, 0.3, 0.4, and 0.5 Hz, with maximum amplitude of 0.5 g. Rotations were at 17 feet from center at $57^\circ/\text{s}$, which resulted in a centripetal force of 0.5 G on the head. Ocular torsion appeared in all four main conditions (acceleration in Y and Z), but with a significant difference in amplitude. No torsion was found in the control condition (acceleration in X), as was expected. The subjects experienced tilt under centrifugation, and indicated a so-called "hilltop illusion" during oscillation. The experience of tilt and ocular torsion were most prominent at the lower oscillation frequencies.

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INTRODUCTION

Surveys spanning the past 30 years and all branches of the U.S. Armed Forces indicate 4-10% of class A mishaps (\$500,000 damage or loss of life): 10-20% of the fatal mishaps were a direct result of spatial disorientation (SD) (Rupert et al., 1990). In addition to aircraft and aircrew losses, substantial costs are associated with mission failures and reduced effectiveness. Recently the Naval Research Advisory Committee (San Diego, 1990) identified SD as the human factor in aviation physical stress having the greatest financial and operational impact on aviation mishaps. Spatial disorientation has been recognized also by the USAF as the most significant human factors problem in aviation mishaps (McNaughton, 1985). Moreover, SD mishap incidence is expected to increase because of increased pilot workload, all-weather flight capability, and reduced proficiency due to reduced flight hours. For the Royal Netherlands Air Force, SD is also thought to be a factor of significance. After the introduction of the F-16, 18 aircraft were lost in 10 years of operational use. Seven of those accidents were attributed to SD (Kuipers et al., 1990).

Although SD is a very complex issue, the above-mentioned facts make it a problem worth solving. In SD, all systems that control eye, head, and body motion are intimately involved: the visual, vestibular, and somatosensory systems, memory of preceding motion, expectation based on planned action, and sensorimotor interactions. The main responsible source of SD, however, is the vestibular apparatus, which is in principle disoriented during transportation by other than self-propelled locomotion. Because of this, a mere vestibularly informed aviator is Type-1 disoriented by definition. Hence, the first approach to the SD problem is to thoroughly investigate vestibular functioning under those conditions that are relevant to aviation.

The present study focused on a major component of the human vestibular apparatus, the otoliths. The otoliths function as linear accelerometers, and are therefore important in our orientation to gravity. They consist of two parts, the sacculus and the utricle, oriented roughly perpendicular to each other. The goal of the present investigation was to reveal the function of these two otolith subsystems, by exposing subjects to linear accelerations from different directions on the body. Because vestibular function is impossible to record in a direct way, it has to be determined indirectly via vestibularly-driven compensatory eye movements or from statements and indications from subjects. We used both methods in this study: 1) measurements of ocular torsion by means of video-oculography, and 2) registration of the subjective vertical by means of joystick indication.

OCULAR TORSION (OT)

During head movements, vestibularly induced compensatory eye movements help to stabilize the retinal image. In the case of lateral head rotations (roll), the vestibulo-ocular reflex results in a (counter) rotation of the eyes about the line of sight, generally referred to as ocular torsion (OT). Ocular torsion induced by static head tilt is attributed to activation of the otolith organs (Miller, 1962; Miller and Graybiel, 1971), whereas the semicircular canals also add OT during dynamic head rotation (Collewijn et al., 1985). Nonvestibular input, such as vision and proprioception from the neck, may contribute as well (de Graaf et al., 1992).

Despite the fact that the otoliths are tilted 30° in the head and their maculae show a certain degree of curvature, functionally, we will treat them as ideally oriented into three directions, X, Y, and Z. With respect to torsional eye movements, our convention will limit response to the total shear force in Y to the utricle, and limit response to the total shear force in Z to the sacculus. When someone is tilted laterally on the tilt chair, the shear force on the maculae of the utricle and the sacculus is then described by the sine and the cosine of the angle of tilt, respectively (Fig. 1a). So both are stimulated, the utricle and the sacculus, but in the literature ocular torsion is often attributed to utricular function alone. From our previous experiments, however, some doubts arose whether this is true. The OT response of 6 subjects to static tilt from upright to 90° is presented in Fig. 1b.

To isolate utricular function from saccular function, this curve was extended to higher G loads (Bos and de Graaf, 1994). Subjects were exposed to an increasing G level in the human centrifuge with the resultant force in Y (stimulating only the utricle, see Fig. 1a). We found a linear relationship between ocular torsion and the G force in the Y direction on the head (Fig. 1b) from 1 to 3 G.

Furthermore, a parabolic flight experiment was performed to obtain the zero point of this 'utricular curve' (de Graaf et al., 1995), where the intercept of the extrapolated line with the vertical axis represented our hypothesis about the position of the eye during weightlessness (where the force on both the utriculus and the sacculus is zero). See Fig. 2.

The mean value of 2.3 degrees ocular torsion (4 subjects, 15 parabolas each) obtained during weightlessness differed significantly from 0 degrees ocular torsion, but not from the extrapolated value of 3.1. The mean ocular torsion values found during the 1-G and 2-G phases of the parabolic maneuver were statistically inseparable from those from the centrifuge data set (and therefore an adequate replication). We therefore concluded that in the range from 0 to 3 G a linear relationship exists between OT and the shear force on the utriculus (F_y), which can be described by $OT = 3.1 + 2.0 * F_y$ (Fig. 3). A comparison with the data obtained during tilt under the normal 1-G condition (open circles of Fig. 1b) suggests that the influence of the sacculus is represented by the offset. To substantiate this hypothesis and to further evaluate the (isolated) contribution of the otolith subsystems to OT, it was necessary to set up a paradigm with accelerations from different directions on the head.

SUBJECTIVE VERTICAL (SV)

The central nervous system uses semicircular canal information to distinguish between a linear acceleration and a tilt (Guedry, 1974; Mayne, 1974). The canals, namely, only respond in the latter case. But, in some cases, a tilt experience could be caused by mere linear acceleration; for example due to prolonged acceleration in the human centrifuge (Clark and Graybiel, 1966; Guedry, 1974). There is also evidence that a brief but strong linear acceleration can generate a tilt percept. During a catapult launch for example, aviators sometimes erroneously experience a pitch-up sensation, which could be disastrous when it is compensated for. This could be due to leak through the low pass (filter) characteristics of the vestibular system (Mayne, 1974).

Our purpose was to investigate this effect for the *lower g-range*: 1) during centrifugation, to obtain a steady-state (reference) tilt percept response, but also 2) during oscillation, to determine the (low pass filter) frequency characteristics of the orienting system. Another aim was to evaluate whether the direction of the acceleration on the head should differentiate the tilt perception (a directional sensitivity).

We set up a paradigm to study the influence of forces from different directions on the otoliths (the utriculus and the sacculus) on eye movements and tilt perception. A question directly relevant to aviation was whether the orienting system does or does not experience tilt during a mild and relatively brief linear acceleration. The stimuli were a horizontal sinusoidal oscillation on a linear track with maximally 0.5 G and a prolonged centrifugation with 0.5 G.

METHODS

Using the Coriolis Acceleration Platform (CAP) of the Naval Aerospace Medical Research Laboratory (NAMRL), five adult male subjects were oscillated in the lateral direction (Y-axis, subject either sitting "upright" or "supine") and in the longitudinal direction (Z-axis, subject "supine" or on his right side) on a linear track. A fifth condition in which the subject was oriented "upright" facing the direction of oscillation (acceleration along the X-axis) served as a control condition. In separate sessions, the same subjects were also rotated (instead of oscillated) in these five orientations. The sinusoidal oscillations were at 0.22, 0.3, 0.4, and 0.5 Hz, with a maximum amplitude of 0.5 G. Rotations were at 17 feet from center at 57 °/s, which resulted in a centripetal force of 0.5 G on the head. Angular acceleration to the steady state was 10 °/s². See Fig. 4 for the design. The order of the conditions was fixed, but the frequencies of the oscillation were balanced between subjects. The runs were performed twice, with a 5-min break in between, the first run was intended for OT measurements only and the second for SV indication.

The subject was tightly strapped and packed with pieces of foam into a chair. His head was immobilized by means of a helmet with individual fit, which was rigidly affixed to the chair. The chair was mounted into a 1.17m³ box. Inside this box it was dark, but after a while the box's inner outlines were (just) noticeable. It was however by no means possible to see anything inside the box (there was, for example, no opportunity for visual feedback from the SV joystick).

Five subjects participated in all five body orientations. Each subject experienced 5 (conditions) x 4 (frequencies) x 2 (OT and SV run) = 40 oscillation runs (of 10 cycles each), and 5 (conditions) x 2 (OT and SV run) = 10 centrifuge runs. During oscillation, the duration of a run depended on the frequency, but it never exceeded 60 s. A centrifuge run lasted 72 s (acceleration and deceleration at $10^\circ/\text{s}^2$ and a steady state at 0.5 g for 60 s). The oscillation and centrifugation runs were executed separately on successive days; the conditions were executed in different weeks (1 week/condition). All subjects except one were naive with respect to the hypotheses of the experiment. We had three dependent variables:

- 1) A verbal report of the experienced tilt. Directly after each run, the subject was asked if he had experienced tilt during the translation, and if so, to estimate its maximum amplitude.
- 2) Subjective vertical (SV), indicated by means of a joystick. The subject was asked to keep the joystick continuously parallel with the gravitational vertical during the run. In effect, this means that a subject will compensate for sensations of tilt (for example, a pitch-down sensation will be indicated by a backward tilt of the stick).
- 3) Ocular torsion (OT): reflexive eye movements about the visual axis, registered with Video-Oculography. The movements of the right eye were continuously registered (50 Hz) on video tape during the run. The eyes fixated on a light emitting diode at 0.81 m to suppress eye movements other than rotation about the visual axis (this was done to overcome the effect of false torsion as a result of large horizontal and vertical eye movements). The recordings were analyzed off line with the algorithm described by Groen et al. (in press). An image during baseline, exactly 3 s before take off, served as reference image.

RESULTS

OSCILLATION

The main finding was that besides translation every subject experienced a certain amount of tilt during the horizontal oscillation. This percept corresponded directly with the appearance of a reflexive torsional eye movement normally associated with tilt (except in the control condition).

- 1) Verbal Report. In conditions A and D, the subjects experienced a tilt in roll; in condition B, a tilt in yaw; and in conditions C and E, a tilt in pitch. The shaded bars of Fig. 5 represent the mean maximum tilt angle of five subjects, experienced on the five conditions. Statistical analysis revealed that only conditions A and D differed significantly from each other (post-hoc Tukey test [$p < 0.01$] on ANOVA: $F = 4.92$; d.f. = 4,16; $p < 0.01$; 38% variance explained): the experienced tilt angle during oscillation was about three times larger in condition A (angle = 11.0°) with respect to condition D (angle = 3.1°).
- 2) Subjective Vertical (SV). Figure 6a shows the raw data from one individual. The data were analyzed as follows: The amplitude of indicated tilt was determined by the mean maximum deflections to either side (peak to peak) of the 10 whole cycles of each run, divided by 2. The dark bars of Fig. 5 therefore represent the mean maximal deviation of the SV from the gravitational vertical, as indicated by five subjects in the five conditions (averaged over the four frequencies of oscillation). A significant difference (post-hoc Tukey test [$p < 0.01$] on ANOVA: $F = 7.45$; d.f. = 4,16; $p < 0.01$; 26% variance explained) was found only between condition A and conditions B, C, and D ($A > B, C, D$). Condition E was not significantly different from any of the others.

No *overall* effect of oscillation frequency was found. An ANOVA, however, did reveal a significant interaction between conditions and oscillation frequency (ANOVA: $F = 2.2$; d.f. = 12,48; $p < 0.05$; 3% variance explained). A post-hoc Tukey test indicated a significant frequency effect ($p < 0.05$) in condition A, in which the experienced tilt (as indicated by the joystick) was most prominent (Fig. 7a).

- 3) Ocular Torsion (OT). Figure 6b shows the raw OT data from the same individual mentioned above. The open bars of Fig. 5 represent the mean maximum (peak to peak/2) OT amplitude of five subjects for the five conditions of body orientation (averaged over the four frequencies of oscillation). All conditions differed significantly (post hoc Tukey test, $p < 0.01$) in OT amplitude, except condition D from B and C. Also a significant ($p < 0.01$) overall frequency effect was found: OT amplitude at .22 Hz > .3 Hz > .4 Hz > .5 Hz (see Fig. 7b):

If the movement of the left eye (not recorded in this experiment) would show a similar pattern as that of the right eye, OT of both eyes should appear conjunctive in conditions A and B (for *both eyes*: a clockwise (CW) torsion due to acceleration to the left, and counterclockwise (CCW) due to acceleration to the right), and disjunctive in condition C and D (for the *right eye*: CCW torsion due to acceleration "upwards," and CW due to acceleration "downwards" for the *left eye*: CW torsion due to acceleration "upwards," and CCW due to acceleration "downwards")¹. For the present purposes, however, only the OT amplitude is relevant, not its direction. Therefore, for the statistical analyses and the presentation in Fig. 7b, values are presented in absolute numbers.

CENTRIFUGATION

During the "steady state" phase of the centrifugation, every subject experienced a static tilt with respect to gravity (Fig. 8) with no remaining percept of horizontal translation.

- 1) Verbal Report. An ANOVA performed on the mean estimates of tilt of the five subjects for conditions A-E revealed no significant differences (17, 22, 30, 23, and 22° of experienced tilt, respectively). The subjects agreed unanimously that the sensation of tilt appeared the strongest in condition C.
- 2) Subjective Vertical. The amplitude of the maximum deflection of the joystick during the run was determined for each condition. The mean results are inserted in Fig. 7a (the steady state "0 Hz" situation). Statistical analysis revealed no significant differences in SV indication between the conditions.

Figure 8 presents the course of SV during the run, averaged over the five subjects. The data show three things:

- (a) an underestimation of the tilt angle (the amount of rotation of the resultant force with respect to the head).
 - (b) at first sight, an asymmetric response between acceleration and deceleration. The course of the build-up of the tilt percept changes more gradually than during the decay.
 - (c) different time constants (τ) between conditions when fitted with a step response of a first order low pass filter (Table 1).
- 3) Ocular Torsion. The amplitude of the maximum OT during the run (compared to the baseline reference image) was determined for each condition. The mean results are inserted in Fig. 7b (the steady state "0 Hz" situation). Statistical analysis revealed a significant difference in OT amplitude between the conditions (ANOVA: $F = 12.6$; d.f. = 4,16; $p < 0.01$; 62% variance explained). A post-hoc Tukey test indicated that conditions A and B (which did not differ from each other) differed from conditions C and D (which also did not differ from each other): OT amplitude was 2-3 times larger in the "utricle" conditions with respect to the "sacculus" conditions. All four conditions differed from condition E, the control condition, where, as expected, no OT was found during the steady state ($OT < 0.2^\circ$).

Fig. 9 presents the course of OT during the run, averaged over the five subjects. The data show:

¹ A recent experiment where both eyes were recorded confirms that this actually is the case (de Graaf et al., 1996).

Table 1. When we fit the centrifuge SV data (presented in the "steady state" situation of Fig. 7a) with a step response of a first order low pass filter [$K = K_0 (1 - e^{-t/\tau})$], this results in a gain value (K_0) and time constant (τ) per condition. Also the low-pass cut-off frequency ($f_{LP} = 1/2 \pi \tau$) is given for each of the five conditions.

Condition	Subjective Vertical		
	K_0 ($^{\circ}/\frac{1}{2} G$)	τ (s)	f_{LP} (Hz)
A	14.4	5.1	0.03
B	11.8	5.9	0.03
C	22.0	7.5	0.02
D	24.4	20.2	0.007
E	15.4	7.5	0.02

- (a) In addition to a static component, in conditions B, C, and E during the phases of acceleration and deceleration a transient OT due to the semicircular canal response to angular acceleration. We doubt that in condition E the tangential acceleration was responsible for OT during the up- and downramp of the profile. The magnitude of tangential acceleration was low ($< 0.1 G$) and would be difficult to separate from the canal-mediated response to the angular acceleration, the latter which was recently reported by Smith et al. (1995).
- (b) For every subject a CW torsion of the right eye in conditions A and B, and a CCW torsion of the right eye in condition C. In condition D, two out of five subjects showed a CW torsion in the right eye.

CONCLUSIONS AND DISCUSSION

First of all, without an adequate visual reference, humans erroneously experience tilt during linear horizontal acceleration with only $0.5 g$! This has been known for a long time in the case of prolonged acceleration. New, however, are the findings obtained during oscillation on the linear track². The tilt percept directly corresponds with the appearance of a reflexive torsional eye movement, normally associated with tilt. The effects are most prominent during acceleration in Y with the subject sitting upright (condition A).

Second, while measurement of eye movements seems of somewhat minor importance for SD investigations, it appears to be a more precise measure than either a verbal report of experienced tilt or a joystick indication. This by no means suggests that the former is of more importance though, only that eye movement data can substantially contribute to a quantitative model of the human vestibular system.

On the basis of results obtained on the tilt chair, during parabolic flights, and during the present experiment on the linear track and the human centrifuge, we may safely conclude that in addition to the utricle, the sacculus also contributes to ocular torsion (although relatively small, there is a response to Z-axis linear acceleration). The 3:1

² At present, we are aware of one similar study, performed at the Massachusetts Institute of Technology (personal communication: Merfeld, 1995). The MIT group investigated OT during oscillation with peak acceleration of $0.7 g$ at four frequencies (0.35, 0.5, 0.75, 1.0 Hz) in conditions equal to our conditions A, B, C, and D. The OT results from both studies are very similar.

ratio in impact between the utricle and the saccule on torsion (together with the notion that while the utricle generates conjugate torsional eye movements, the saccule may generate disjunctive torsional eye movements) sufficiently explains the course of ocular torsion during tilt under normal 1-G conditions (the first part of the curve of Fig. 1b). Also an indication is given about the behavior of the eyes in an aviator-relevant, higher than 1-G environment, it might be possible that a pilot during $+G_z$ has to not only suppress an ongoing vertical upbeat nystagmus (Marcus et al., 1989; Marcus and Van Holten, 1990; McGrath, 1993), but also a cyclo-vergence of the eyes. At the lower G level, this cyclo-vergence of the eyes may slightly hamper the pilot's ability for stereoscopic vision in depth. At the extreme G levels, it could eventually ruin ocular fusion completely.

Third, the frequency effect observed in our data set elucidated a parameter setting of particular interest, namely the cut-off characteristics of the low-pass filter in human spatio-temporal orientation. This parameter is not only relevant as a "built in" potential source of disorientation, about which every aviator has to be informed of, but is also relevant for the world of flight simulation. For training purposes, the fine tuning of the intended flight profile to these low-pass filter characteristics of the human perceptual system is of evident importance if one wishes to validate the simulation to the real world. A fit of the OT and SV data from centrifuge and linear track with a first order low-pass filter gain function, reveals time constants (τ) that seem to differ somewhat between conditions (see Table 2).

Table 2. When we fit the OT and SV data from pooled centrifuge and linear track runs, as presented in Fig. 7a and b, with a first-order low-pass filter gain function $[K_0/\sqrt{1+(2\pi f\tau)^2}]$, this results in a gain value (K_0) and time constant (τ) for each condition. Also the low-pass cut-off frequency ($f_{LP}=1/2\pi\tau$) is given for each of the five conditions.

Condition	Ocular Torsion			Subjective Vertical		
	K_0 ($^\circ/1/2 G$)	τ (s)	f_{LP} (Hz)	K_0 ($^\circ/1/2 G$)	τ (s)	f_{LP} (Hz)
A	2.9	1.4	0.12	15.0	1.4	0.12
B	3.5	2.7	0.06	12.2	2.7	0.06
C	1.4	2.5	0.06	21.3	4.7	0.03
D	2.2	3	0.05	23.0	6.6	0.02
E	0.3	1	0.16	18.0	3.0	0.05

When we compare the SV-time constants based on the fit through the combined centrifuge and linear track data (SV_{frequency response}, Table 2) with the SV-time constants obtained from the centrifuge data, only (SV_{step response}, Table 1) the proportion of the difference in τ between conditions (within the sets) appears equal, but the magnitudes themselves do differ substantially between the sets. This is disappointing, since the two sets of SV-time constants should provide information about the same underlying mechanism! Maybe this discrepancy could be caused by substantial noise due to the SV-indication procedure itself, as could happen, for example, when subjects are unable to maintain a stable response criterium. However, the method has proven its use in the past, and there are definitely more probable alternatives that can account for the discrepancy in magnitude of τ between the sets of Tables 1 and 2. During the centrifuge run, the subjects were exposed to transient dynamic forces during the acceleration and deceleration phases. Perhaps these angular and tangential components had a confounding influence on the subject's perception at that stage. Such difficulties may interact with (and may delay) the joystick indication. Another explanation could be that too few data points were gathered to yield a valid fit between the centrifuge and linear track data sets. If this were true, we should fill the region with data from new oscillation runs between 0.0 and 0.22 Hz.

Finally, we can say something about the relationship between OT and SV. A comparison within condition A, where the axes of rotation for OT and SV are the same (the resultant gravito-inertial force rotates in the roll plane), shows similar time constants. This is, however, much less evident for condition D, where the gravito-inertial force also rotates in the roll plane. We, however, do not think that this is an indication that the sacculus serves a different function for tilt perception than for OT; from the sections above, we already know that with respect to OT there does exist a weighting in favor of the utricle (of about 3:1), and this also seems to be the case for SV (at least for oscillation). Moreover, the OT time constant in condition D is longer than in condition A. Hence, we may better conclude that for both the responses, OT and SV, the saccular system responds differently than the utricular system. For SV, the differences in buildup of the tilt percept between "utricular" (A and B) and "saccular" conditions (C and D) are presented in Fig. 8. In condition E, we anticipated a low correlation between OT and SV because the otoliths function in 3-D for SV, but only in 2-D for OT (the YZ- or frontal plane). Therefore no OT was expected in condition E, where the subject was accelerated along his X-axis (and because of the very low gain, the other parameters in this row of Table 2 are of no importance). If one is interested in the straight correlation between perception of tilt and vestibularly generated eye movements, one has to take all the (3-D) eye movement components into account and not restrict oneself to OT. In the case of condition E, the amplitude of the vertical linear VOR should then be the relevant measure. At present, our interest focused on only the OT component, and therefore the determination of such a general relationship for three dimensions could never be the goal of this study. A comparison of the results from the other four conditions, however, gave enough reason to appreciate the idea of one common underlying mechanism for OT and SV. Both seem to simply respond to the shear force on the otolith maculae, with the same low-pass filter characteristics and the same weighting (3:1) in favor of the utricle.

The present experiment raised two new questions. The first concerns the character of the torsional eye movements generated by a high + G force in Z (e.g., during a coordinated turn). As mentioned above, a cyclo-vergent eye movement could be a serious threat to stereoscopic vision. Its impact could easily be investigated with the centrifuge by measuring of the behavior of both eyes under increasing hyper gravity conditions. The second topic of interest is the response of the human vestibular system to oscillations in the range lower than 0.22 Hz; the gap which still exists between steady state ("0 Hz") and 0.22 Hz (Fig. 7). Because one of the great virtues of the linear track on the CAP, namely its length, already approached the limits during the present experiment, a still lower frequency could only be achieved by means of a trick. With a combination of translation on the track and a simultaneous rotation of the whole device, it is possible to enter the lower frequency range. With respect to our experiment during mere oscillation, the presence of the Coriolis force may however be a confounding factor. Therefore, a comparison of data obtained during similar frequencies (for example 0.22 and 0.3 Hz) in both paradigms (with or without simultaneous rotation) will give an indication about the eventual influence of this Coriolis force. This way on the CAP, it must be possible to obtain additional and relevant data points (say at 0.11 and 0.17 Hz, with a maximum acceleration of 0.5 g). This may help to overcome the uncertainties, mentioned above, in the determination of which time constant is the more correct, and thus will contribute to a quantitative upgrade of our human spatial orientation model.

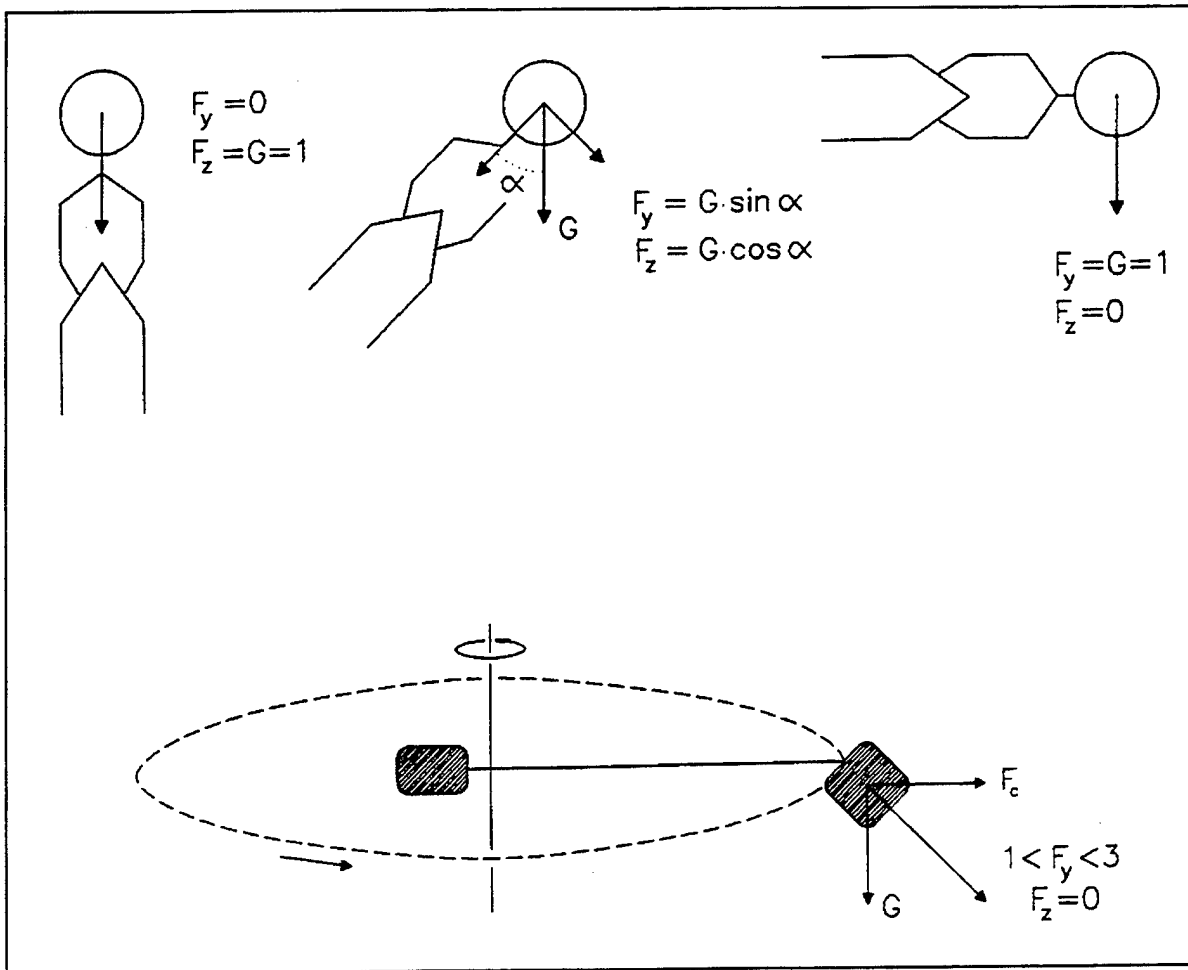


Figure 1a. The shear force produced on the maculae of the utricle ($F_y = G \cdot \sin \alpha$) and the sacculus ($F_z = G \cdot \cos \alpha$) during tilt, and during centrifugation in a human centrifuge with the subject's head oriented in Y on the resultant G force ($1 < F_y < 3$; $F_z = 0$).

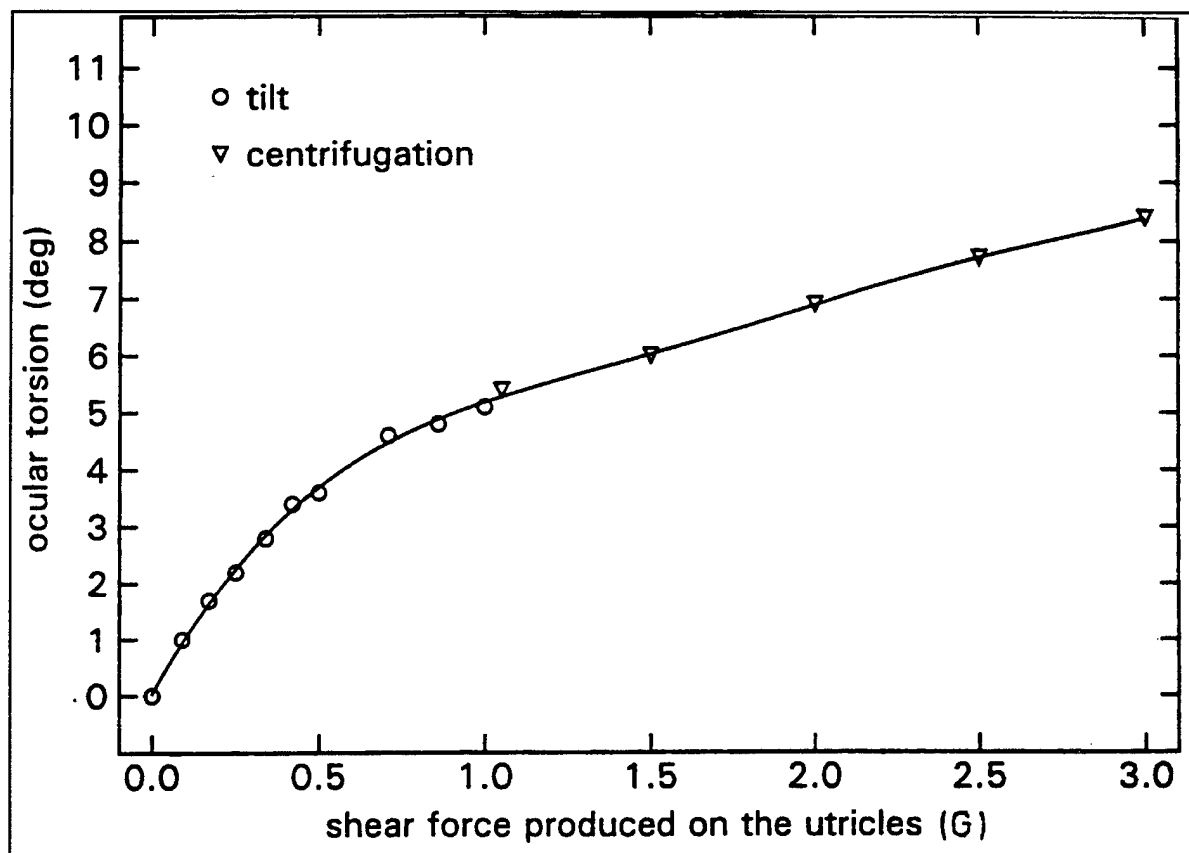


Figure 1b. Mean OT of 6 subjects. The first part of the curve (from 0.0 to 1.0 G, open circles) represents the effect of tilting the subject laterally on the Tilt chair, while the second part (from 1.05 to 3 g, open triangles) represents OT as a function of centrifugation.

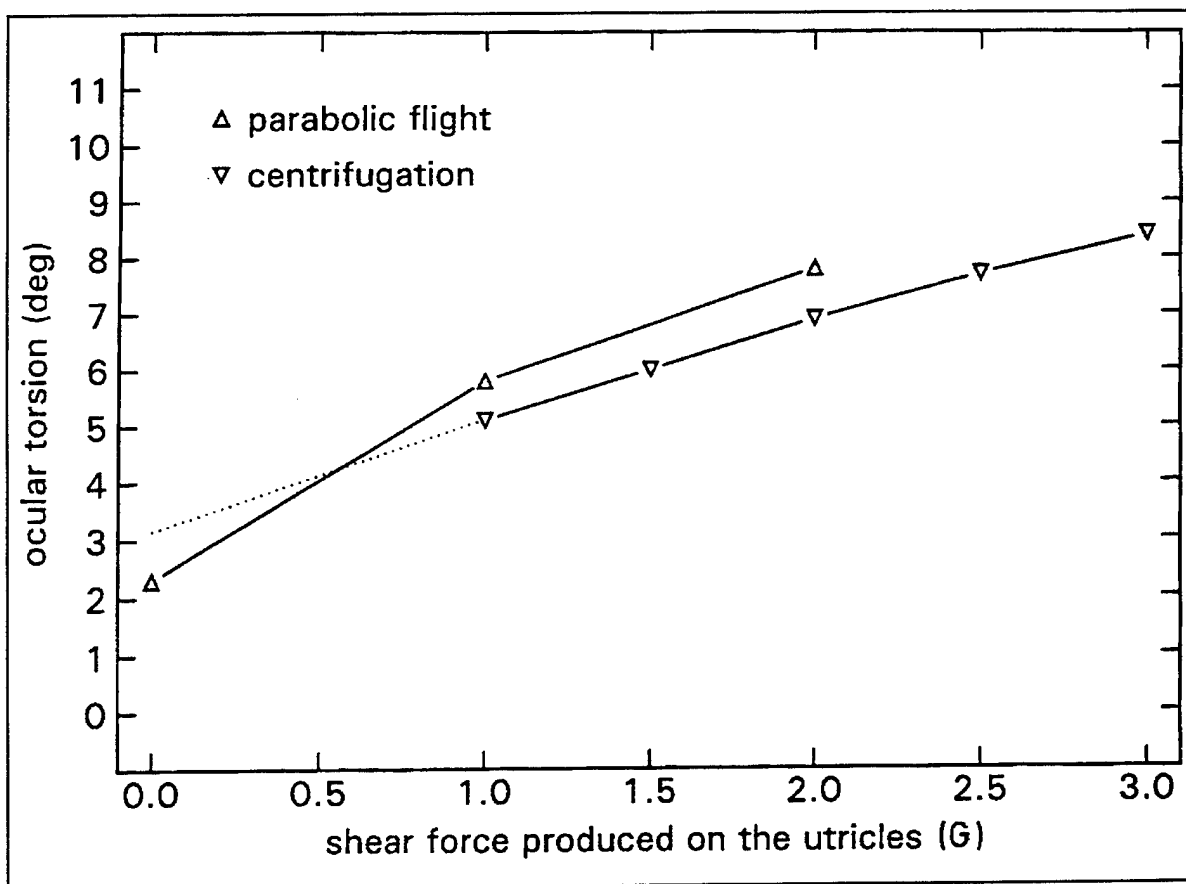


Figure 2. Ocular Torsion data from the centrifuge experiment in which the (resultant) G force was increased from 1 to 3 G in increments of 0.5 g . The intercept of the extrapolated (dotted) line with the vertical (OT) axis represents a hypothesis about the position of the eye during 0 G . Also the mean OT data actually found during the 0-, 1-, and 1.8- G phases of the parabolic maneuver are shown.

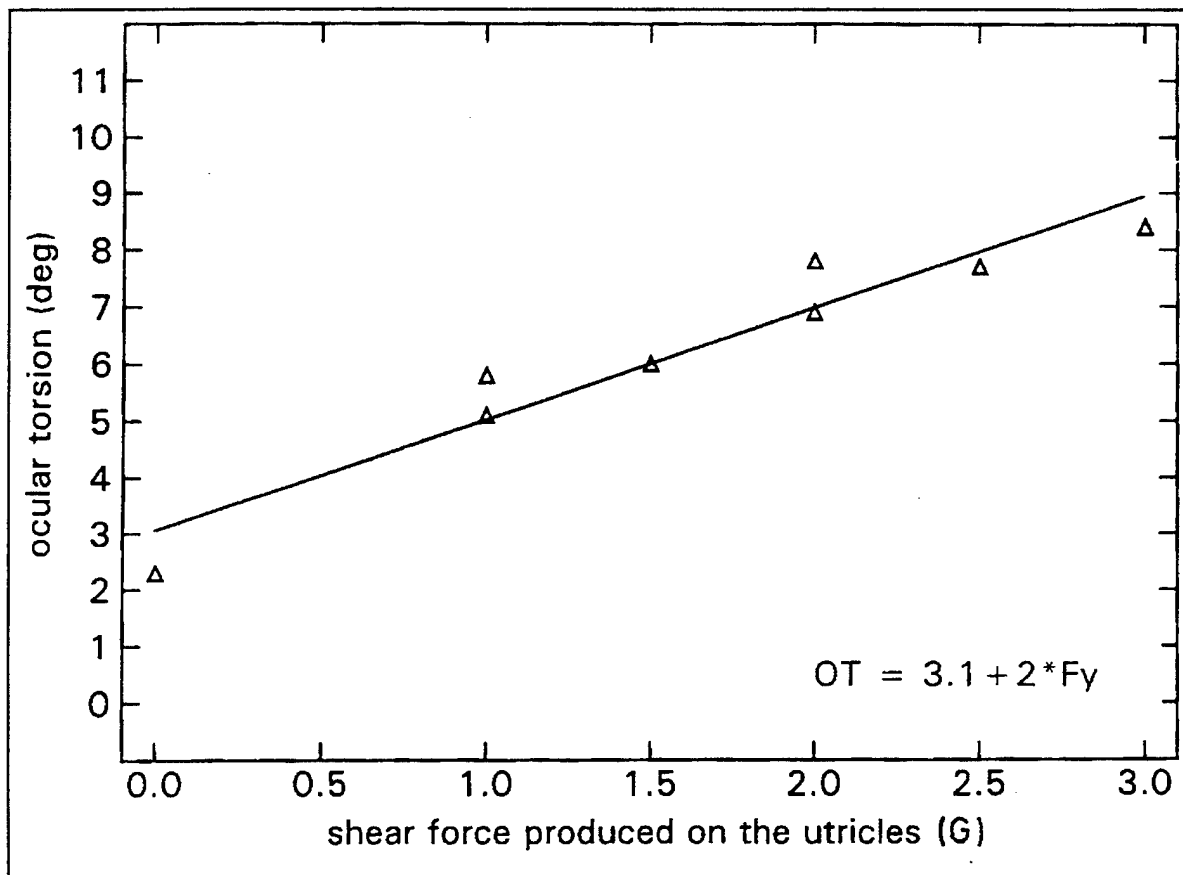


Figure 3. A pooling of the data from centrifuge and parabolic flight experiments revealed a linear relationship between OT and the shear force produced on the utricle.

	A	B	C	D	E
OSC	$G_x = 0$ $G_y = \text{var}$ $G_z = 1$	$G_x = 1$ $G_y = \text{var}$ $G_z = 0$	$G_x = 1$ $G_y = 0$ $G_z = \text{var}$	$G_x = 0$ $G_y = -1$ $G_z = \text{var}$	$G_x = \text{var}$ $G_y = 0$ $G_z = 1$
ROT	$G_x = 0.1$ $G_y = -0.5$ $G_z = 1$	$G_x = 1$ $G_y = -0.5$ $G_z = 0.1$	$G_x = 1$ $G_y = 0.1$ $G_z = 0.5$	$G_x = -0.1$ $G_y = -1$ $G_z = 0.5$	$G_x = 0.5$ $G_y = 0.1$ $G_z = 1$

Figure 4. The experimental design. Condition A to E: The five body orientations. Oscillation (OSC): Var, the maximum level of acceleration (in g) during sinusoidal oscillation $= 0.5 \sin 2\pi ft$. The four oscillation frequencies (f) are 0.22, 0.30, 0.40, and 0.50 Hz. Rotation (ROT): the tangential acceleration is given for the upramp of the centrifugation. The forces indicated conform to the physiological reaction nomenclature described in Hixson et al., 1966.

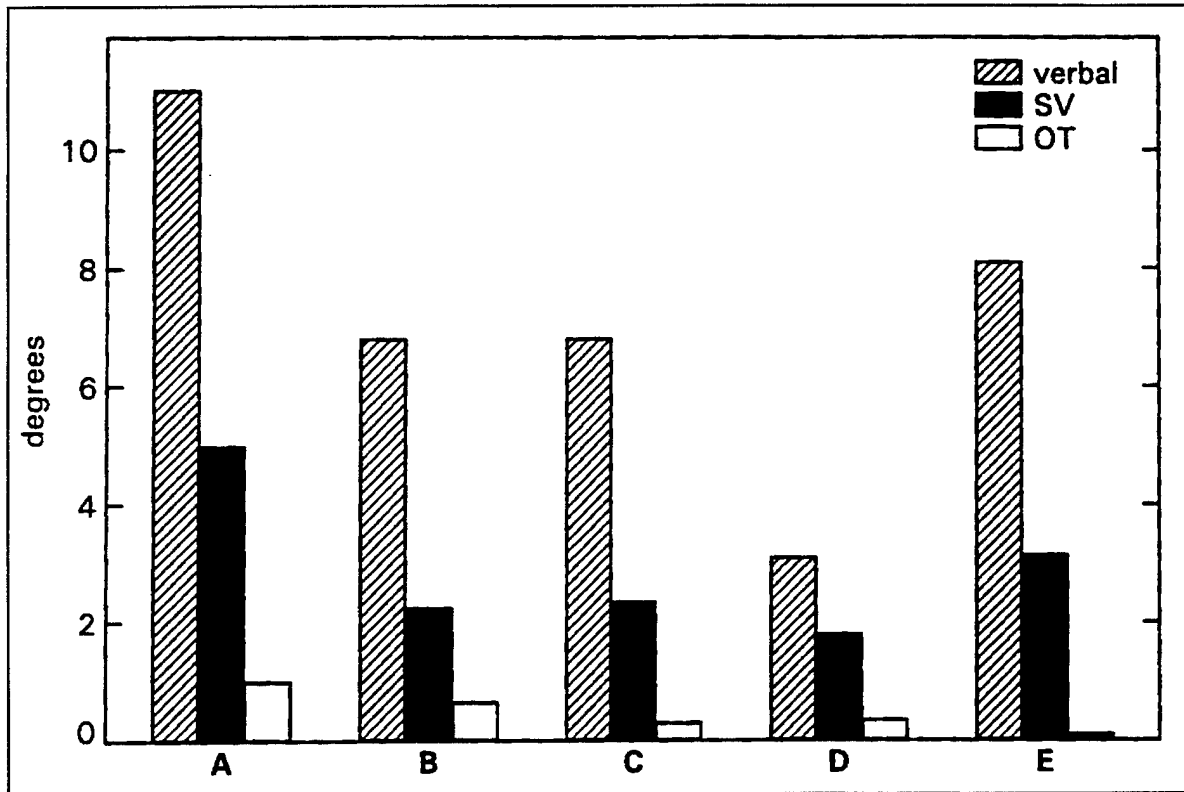


Figure 5. Horizontal oscillation. The combined results of verbal report, joystick indication and ocular torsion for the five conditions.

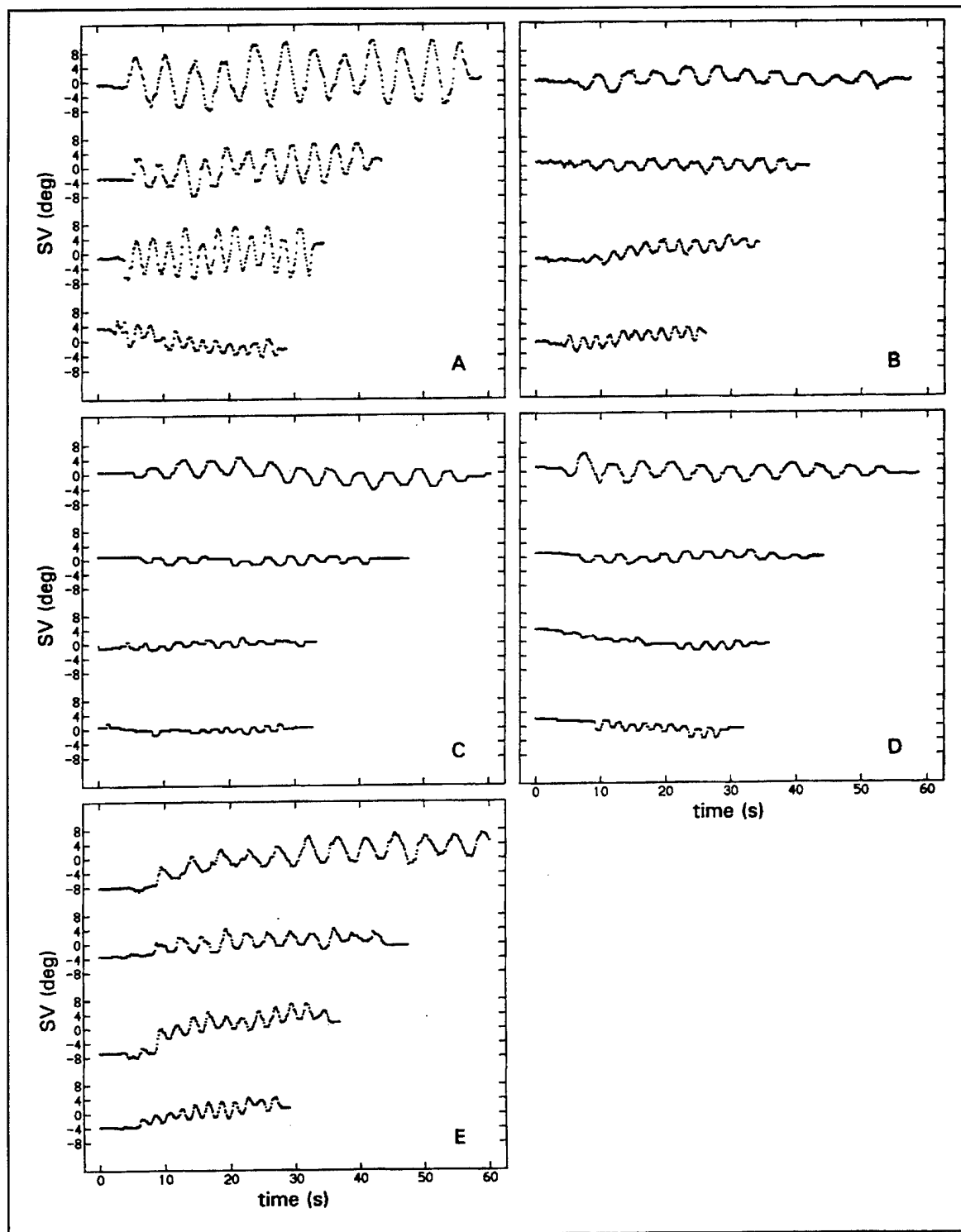


Figure 6a. Raw SV data (6a) and OT data (6b) from one individual (sample frequency as shown = 10 Hz). Condition A to E: oscillation frequency from top to bottom: 0.22, 0.3, 0.4 and 0.5 Hz, respectively.

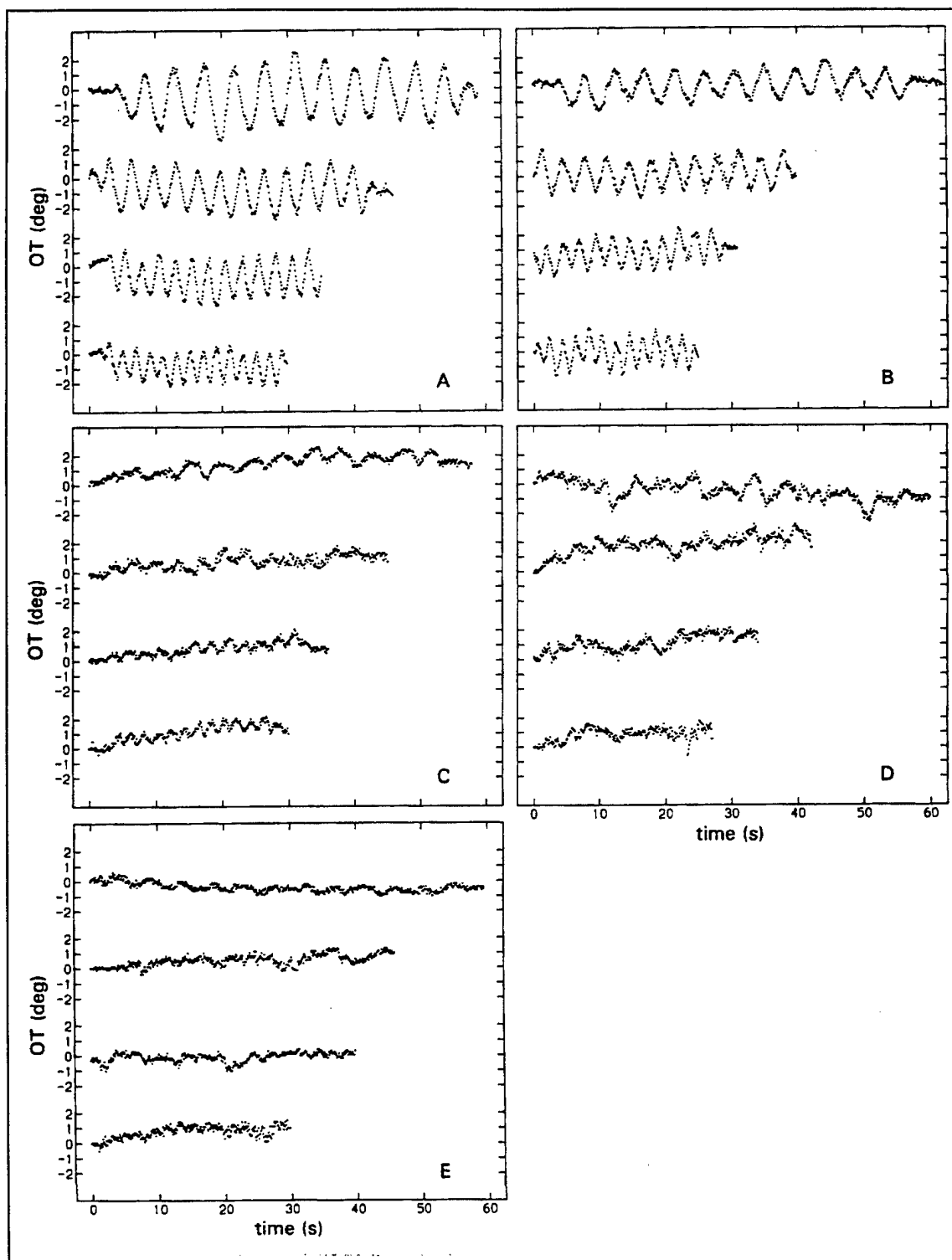


Figure 6b. Conditions A to E. Oscillation frequency from top to bottom (0.22, 0.3, 0.4, and 0.5 Hz, respectively)

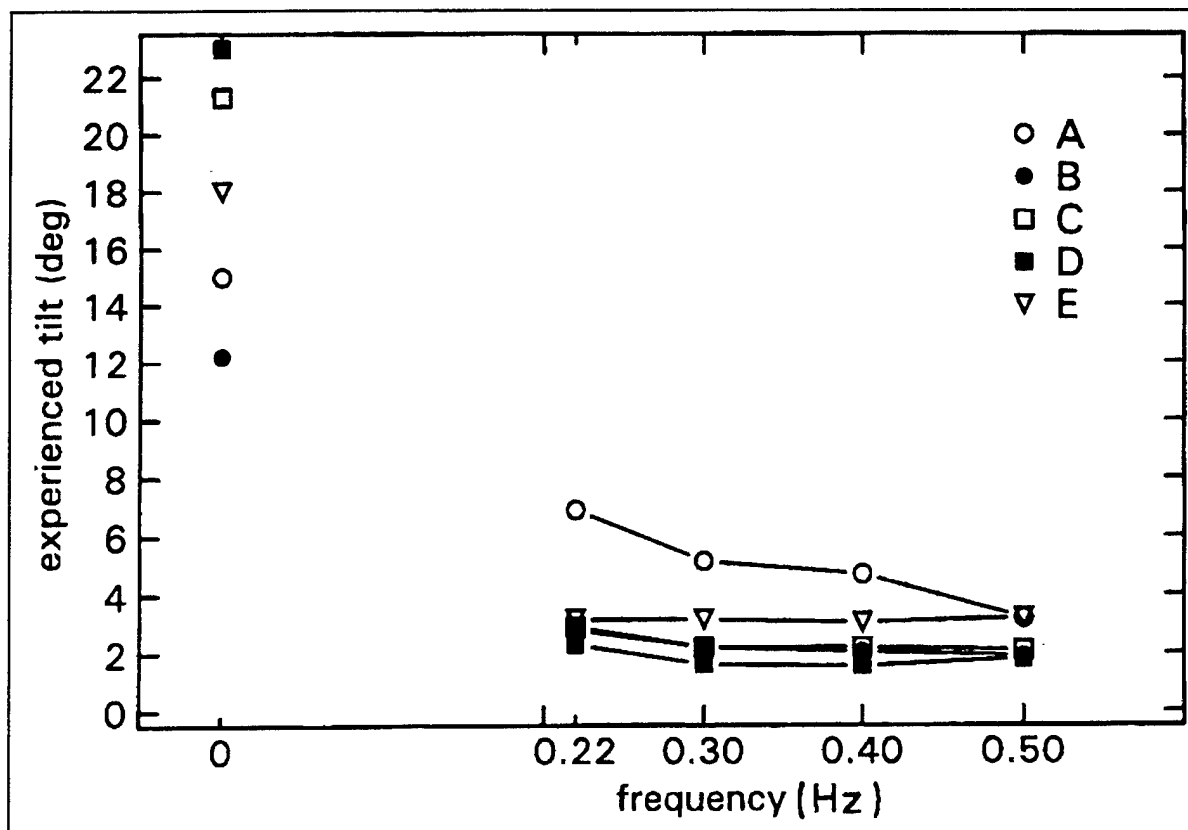


Figure 7a. Mean SV data (7a) and OT data (7b) per condition (A to E) against oscillation frequency. The results from centrifugation are also given ("0 Hz"). OT and the experience of tilt were most prominent at the lower frequencies and somewhat noticeable at the higher frequencies

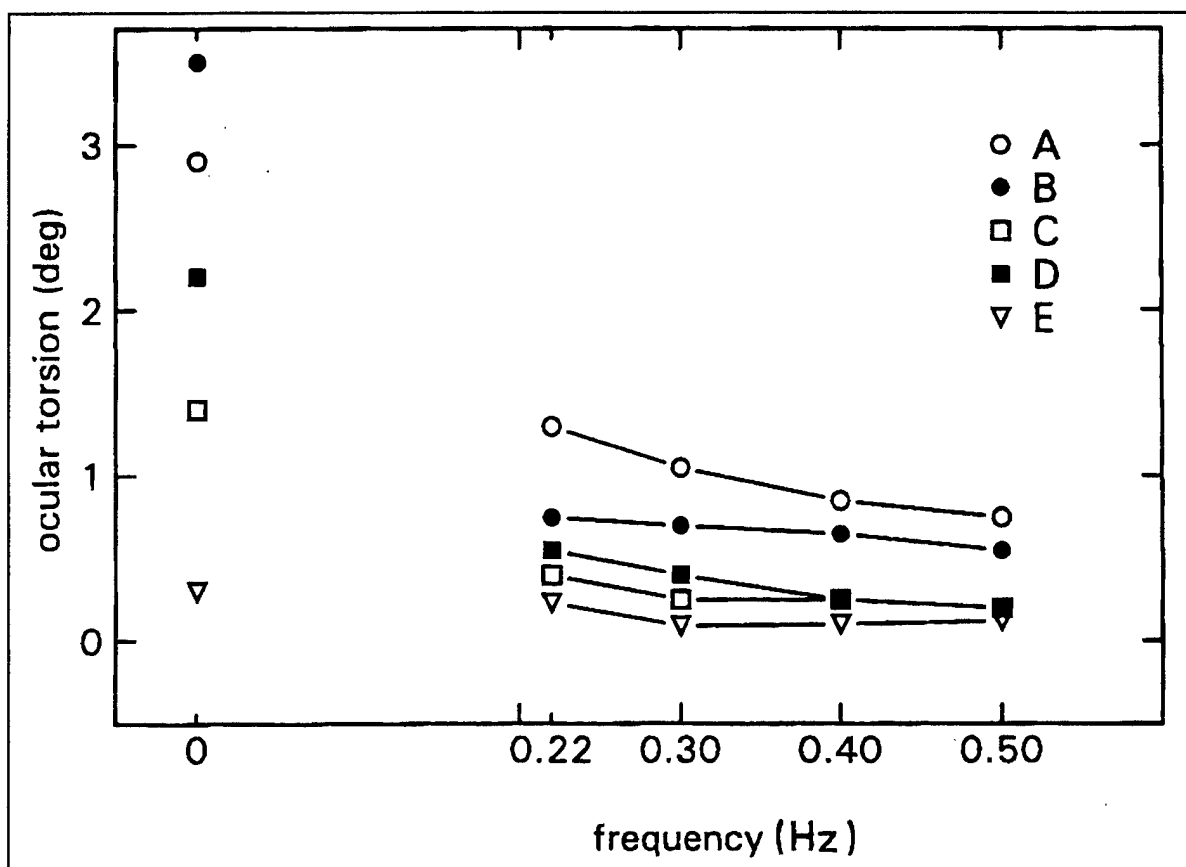


Figure 7b. OT data.

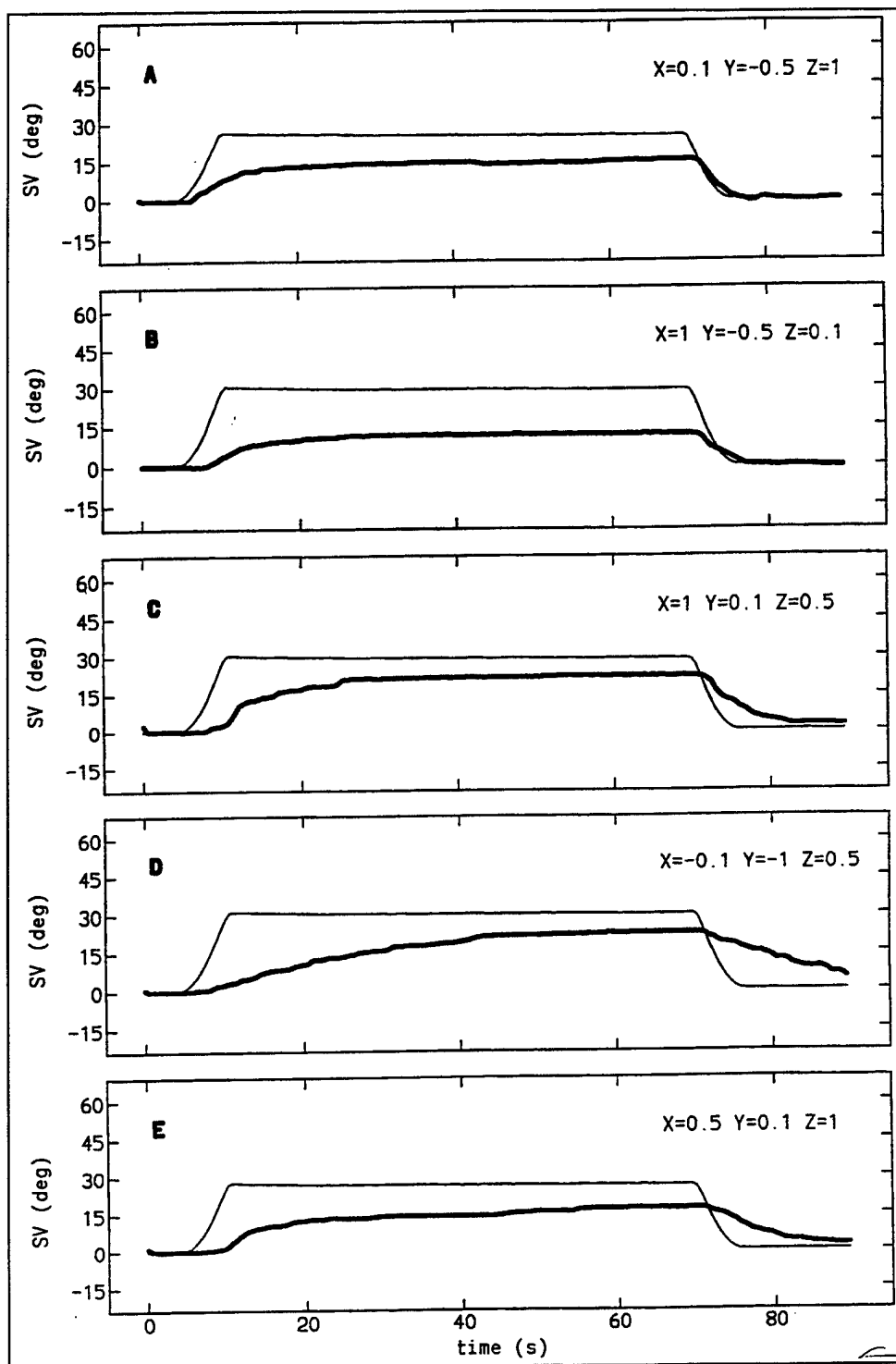


Figure 8. Mean SV indication from five subjects during centrifugation in conditions A-E. The thin line represents the amount of rotation of the resultant force with respect to the head (26.6° during the steady state). Notice the gradual build-up of the tilt percept, and the underestimation of tilt in all five conditions.

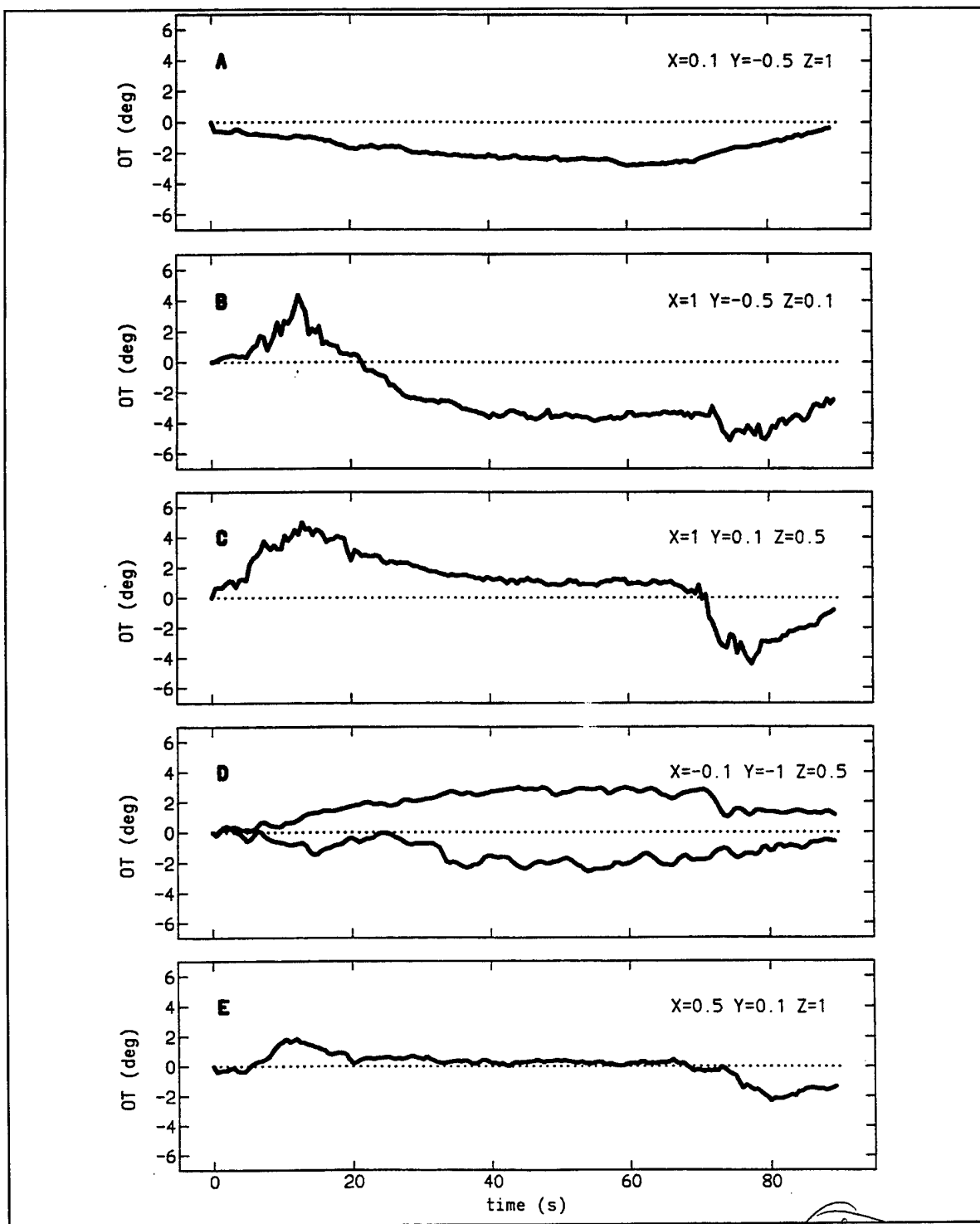


Figure 9. Mean OT of the right eye from 5 subjects during centrifugation in condition A to E. An image during baseline, a few seconds before take off, served as reference image. A positive OT stands for CCW rotation (to the left) of the eye as seen from an observer standpoint. In condition D the subjects behaved somewhat divergent (see text), therefore only the curves of those with the same OT behavior are averaged.

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13. ABSTRACT (Maximum 200 words) Humans perceive linear acceleration and tilt by the otoliths as a result of shear forces on the maculae. A paradigm was set up to study the influence of forces from different directions on the otoliths, on eye movements and tilt perception. On the Coriolis Acceleration Platform of the Naval Aerospace Medical Research Laboratory (NAMRL), five adult male subjects were oscillated in the lateral direction (Y-axis, subject either sitting "upright" or "supine") and in the longitudinal direction (Z-axis, subject "supine" or on his right side). A fifth condition, in which the subject was oriented "upright" facing the direction of oscillation (X-axis), served as a control condition. In separate sessions, the same subjects were also rotated in these five orientations. Data were obtained by measuring ocular torsion with video-oculography, and the direction of the subjective vertical was recorded by means of a joystick. The sinusoidal oscillations were at 0.22, 0.3, 0.4, and 0.5 Hz, with maximum amplitude of 0.5 g. Rotations were at 17 feet from center at 57°/s, which resulted in a centripetal force of 0.5 G on the head. Ocular torsion appeared in all four main conditions (acceleration in Y and Z), but with a significant difference in amplitude. No torsion was found in the control condition (acceleration in X), as was expected. The subjects experienced tilt under centrifugation, and indicated a so-called "hilltop illusion" during oscillation. The experience of tilt and ocular torsion were most prominent at the lower oscillation frequencies.				
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